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EFFECTS OF TEMPERATURE, SALINITY, AND SURFACE WATER FLOW ON DISTRIBUTION OF THE SEA SNAKE PELAMIS[1]

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ABSTRACT
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The pelagic yellow-bellied sea snake Pelamis platurus is a surface feeder which apparently drifts passively with surface currents. In areas of horizontally convergent surface water flows, hundreds or even thousands of Pelamis are concentrated in slicks, apparently characteristic members of a community of organisms associated with slicks.
The distribution of Pelamis in the tropical Indian and Pacific Oceans is correlated with surface water temperatures; colonization of the Atlantic Ocean has likely been prevented by low surface temperatures off the tips of South Africa and South America. Breeding populations apparently occur only in areas in which mean monthly temperatures exceed 20C. The upper lethal temperature of Pelamis is about 33C. Thermoregulatory diving may be a mechanism of avoiding heat death in tropical seas where surface water temperatures reach 31C and insolation is intense.
Pelamis can survive in freshwater for periods longer than 6 months.
INTRODUCTION
We are deeply appreciative to the governments of Mexico, Costa Rica, and Panama coastal waters. Drs. Harold Voris, B. Villa-R, and Michael Murphy kindly provided assistance during various phases of these studies.
bellied sea snake Pelamis platurus might
The possibility that the poisonous yellow- for permission to collect snakes in their colonize the Atlantic Ocean through the proposed Atlantic-Pacific sea level canal (Sullivan 1970; Rubinoff 1970; Rubinoff and Kropach 1970) has stimulated interest in the means by which sea snakes have uccessfully adapted to a life completely at ea and in the factors important in controling their distribution. We have examined come effects of temperature, salinity, and surface water flow on survival and movements of Pelamis in the eastem Pacific Ocean.
Financial support was provided by National Science Foundation Grant GB-16653. Portions of this study were carried out on board the RV Alpha Helix with NSF support.
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MATERIALS AND METHODS
Sea snakes were collected during a land-based study along the Pacific coast of Mexico between Puerto Arista (Chiapas) and Barra de Navidad (Jalisco) in July and [AD] August 1970-1971. On a cruise of the RV Alpha Helix between San Diego and Panama (29 August-14 September 1970) additional information and specimens were

collected off the coasts of Mexico, Costa Rica, and Panama. The snakes show little
NOVEMBER 1971, V. 16(6)

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fascinating and talented maritime people. It is hardly possible that their culture perished entirely when Santorin erupted. There is much evidence in the Mediterranean and European cultures to lead one to believe that it was perhaps scattered as seed on the wind in that cataclysm.

How Sea Snakes May Avoid the Bends

NE OF THE PROBLEMS confronting any diver is the bends-the slow build-up of gaseous nitrogen in the blood and tissues during a dive and the need to remove it before surfacing. Too rapid an ascent results in nitrogen bubble formation in the blood, which can lead to considerable body damage and even death.

For several years, scientists have been examining the diving biology of sea mammals to find out how they avoid the bends. In general, these animals undergo bradycardia, a physiological state in which the heartbeat slows, the lungs are emptied of air, blood flow is reduced to all but the most critical parts of the body, and the muscles are allowed to respire anoxicly. All of this is designed either to reduce the amount of gaseous nitrogen in the body or to minimize its entrance into critical areas.

The diving physiology of another animal, the sea snake, has been the subject of an investigation by Roger S. Seymour of Monash University at Clayton, Australia. He has found that

these reptiles use an entirely different system to achieve the same results. In the sea snake, the lungs remain full during a dive, but the dangerous nitrogen is prevented from reaching the rest of the body by a shunt in the circulation system.

Normally, blood flows in a big

double loop centered on the heart- from the lungs to the heart to the body to the heart and so on. Sea snakes, however, have what is essentially a "hole" in their heart; therefore, during a dive, blood from the body bypasses the lungs altogether. By this means, the blood is not greatly exposed to the nitrogen-rich air, and only the lung tissues are affected by nitrogen build-up.

The small amount of the gas that does reach the body proper diffuses through the permeable skin of the reptile at a rate that increases with depth. The total result is a constant low level of nitrogen in the body. Thus, when the sea snake surfaces, only the lung tissues, which gain and lose gases rapidly, need degas.

Sea Frontiers

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TABLE 1. Tolerance of Pelamis to high tempera-
TABLE 2.
Tolerance of Pelamis to low tempera-
tures
tures
pax
Body wt
(g)
(°C)
Seawater temp Exposure time
(days)
Survival
Freshwater temp
(°C)
Exposure time
847
(days)
Survival
66.4
35.4
0.52
24.0-26.0
260.0
14.7
35.2
0.79
19.8-20.4
>16.9

22.9
35.2
0.79
19.8-20.4
>16.9
53.5
34.8
2.08
19.8-20.4
0.8
51.5
34.2
0.87
18.8-19.0
2.0
45.6
33.6
0.60
18.8-19.0
2.0
47.7
33.6
2.00
18.5-19.0
4.1
47.7
33.2
0.92
18.5-18.8
6.3
69.7
32.8
17.9-18.3
2.91
>15.8
17.9-18.3
45.4
32.0
4.02
10.8
15.9-16.6
64.0
28.8
14.1
>19.8
+++1+1++I+
15.9-16.6
9.9
Dead, alive +.
15.9-16.6
5.9
15.9-16.6

0.9
14.0-14.8
11.5
14.0-14.8
4.8
12.8-13.3
5.0
12.8-13.3
3.9
10.4-11.0
2.8
10.4-11.0
1.8
1.2
1.2
FIG. 1.
Distribution of Pelamis platurus () in relationship to the 20C mean surface seawater isotherms in August (dashed line) and February (solid line). The stippled portion, representing an area which has no month in which the monthly mean is less than 20C, closely corresponds with the best present estimates of Pelamis breeding range (excluding the Atlantic Ocean and Red Sea which have no snakes).

reaction to vessels and were easily dip- whitish infection of the skin which develnetted from a small boat.

The cloacal temperatures of snakes in the wild were taken with a Schultheis thermometer. The position of these snakes and the associated slick was calculated from sextant sightings of the shoreline. In laboratory studies of temperature tolerance, the snakes were first acclimated for 2-6 weeks to 22.5-26.5C and then exposed to seawater or freshwater of various temperatures in an incubator or constant temperature room while fasting.

Survival times during forced diving were measured in freshwater with snakes confined to the bottom of a glass jar.

In laboratory studies of freshwater tolerance, snakes were maintained in tapwater in plastic cans lined with polyethylene bags. The water was filtered continuously and changed once a week. The snakes were fed goldfish held with tweezers. A persistent oped in snakes kept in fresh- or seawater was successfully treated with Aquari-sol (soluble Ag■O) and tetracycline.

Subsurface temperature profiles were taken with a mechanical and an expendable bathythermograph. Salinities were determined with a chloride titrator.

RESULTS AND DISCUSSION

Distribution and sea surface temperatures

Pelamis is a cosmopolitan species and has by far the widest range of any sea snake. A plot of collection records (Fig. 1) reveals that this serpent is widely distributed in tropical seas except for the Atlantic Ocean. Red Sea, and central Pacific (Smith 1926). Because Pelamis is a passive surface drifter. it is often wafted by currents into latitudes in which it is not a breeding resident. Records from Hawaii, the Galápagos Islands, the Sea of Japan, the tip of South Africa, Tasmania, and New Zealand (Halstead 1970) all seem to be marginal records of snakes wafted beyond their breeding range. A persistent search for Pelamis was made in the vicinity of the Galápagos Islands in 1968 (6 weeks) and in 1969 (2 weeks), but no trace of them was found. Fitzsimons (1962) reported that Pelamis has been found in South Africa as far west as Table Bay (near Cape Town) which is actually in the South Atlantic, but he pointed out that these records are of occasional stray specimens. Along the east coast of South Africa there is a transition from a subtropical to a warm temperate fauna near the mouth of the Bashee River on the Transkei coast (about 32° S lat) (Day 1969). Snakes carried as far west as Table Bay actually enter a cold temperate zone in which survival is only temporary. New Zealand, Tasmania, and Japan are also too cold for
year round
presence of Pelamis.

Low temperatures are not a barrier to dispersal in Hawaii, and we do not know what factors restrict their colonization of these waters. Along the west coast of South America, the most southerly sea snake populations are found near the Santa Elena peninsula at the Gulf of Guayaquil, Ecuador, at 3-5° S lat (J. Peters, personal communication). A plot of 20C surface isotherms (Fig. 1) clearly reveals an intrusion of cool water from the south along this coast (Sverdrup et al. 1942). Our best estimate
5.7-7.0
5.7-7.0
Dead ; alive +.

of the breeding range of Pelamis falls within the boundaries of the February isotherm to the north and the August isotherm to the south. February in the northern hemisphere and August in the southern hemisphere are usually the coldest times of the year. Thus temperature appears to be a major limiting factor for Pelamis and may account for the absence of this snake from the Atlantic Ocean. The surface temperatures off the southwest coasts of Africa and South America are apparently lower than the animal can tolerate, so colonization is prevented.

Temperature tolerance

In a group of 11 snakes tested at high temperatures in seawater, the upper lethal temperature seemed to lie between 33.2 and 33.6C (Table 1). Thus Pelamis could not be expected to survive indefinitely at temperatures much in excess of 33C (about 91F). In another series, 13 snakes were tested in air rather than in water; 12 died within 12 hr at temperatures between 35.4 and 43.4C; one survived for 12 hr at 34.2C. There seems to be little difference between 2'

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28.7 28.5
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28 28.0-
28.5
28.5
28.4
27 27-
27.7
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27.0
28.3 28.4
28.3
28.4
26.0.

26 26.
26.0
28.0.
28.4 28.4
26.01
25 25.01
25.0 25.0 24.6
-28
27.0
24,0 24.0.
25
25,0.
25.0
24.0
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23.7
22.4
23.0
24.0
21-8 -22
227
23.0
23.0
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20.0°
20
20-6
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19.0
20.0
19.
9.0.
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18.1
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17.0 17.0
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17.0
16
16.0
16.2
15.8
15.5
16.0
air and water in the upper limits tolerated. Twenty-one recently born Pelamis (9.5-14.3 g) tested for cold tolerance showed considerable variation in response (Table 2). Some of the deaths were undoubtedly due to the conditions of captivity, so it is probably more important to consider the longest survivals at a given temperature rather than mean mortality rates. It seems clear that below 13C survival was less than 5 days (Table 2). At 14.0-14.8C, one snake survived for 11.5 days, quite a creditable period; another lived for more than 19 days at 15.9-16.6C, two each lived for long periods at 17.9-18.3C and 19.8-20.4C, and at 24.0-26.0C eight survived for more than 6 months. Although it is not possible to define the lower lethal limit, it appears to be below 20C, possibly between 14.5 and 17.0C. This seems compatible with the theory of limitation of breeding range by the 20C isotherm, since reproduction may well require temperatures above that of the lower lethal level. Snakes living along the 20C mean isotherm are of course exposed to lower temperatures from time to time.

Body temperatures

During a cruise of the RV Alpha Helix more than 500 Pelamis were caught in surface waters that varied from 26.9-31.0C. The highest surface temperatures were recorded in Bahía Petacalco, Mexico (17° 51'N lat). Snakes in these waters seemed perilously close to their upper lethal level, suggesting that some type of behavioral thermoregulation might be necessary to avoid heat death. These snakes spend a great deal of time at the surface and their black backs are not always completely submerged. This might be an advantage for basking at water temperatures cooler than preferred, but when the water temperatures are near 31C, the heat gain from solar radiation might be sufficient to cause death. There are two obvious ways to lose heat:

by evaporative cooling or moving into cooler waters. Evaporative cooling seems unlikely in an animal which already has a problem conserving water (Dunson et al 1971; Dunson 1968, 1969). On the othe hand, cooler water is close at hand if the snakes can dive into the upper portion of the thermocline. The thermoclines in the areas studied were usually found at depths of 25-60 m, but water at least a few degrees cooler than the surface could be found at lesser depths (Fig. 2). This raises the question of how deep Pelamis actually does dive. Sea snakes are of course air breathing, but they are rather tolerant of anoxia associated with diving. When 11 bal Pelamis were forced to dive in freshwat (26-29C), four lived from 0-2 hr, five fro 2-4 hr, and two from 4-5.5 hr. With four snakes tested at a water temperature of 13C, survival was considerably longer: two lived for 4-10 hr and two for 10-24 hr Thus it seems that Pelamis has the ability to survive dives of extended duration.

While we were netting wild snakes, we often saw individuals dive out of sight quickly when touched. Although direct measurements of diving snakes are neede to determine the actual depths and dur. tions of these dives, we may be able to infer the existence of thermoregulatory diving from some activity temperature data. On 10 September 1970, at Bahía Piñas. Panama, we took cloacal temperatures of 31 freshly captured Pelamis and compared them with water temperatures. Surface seawater temperatures taken at this time (1530 to 1730 hours) varied between 28.2 and 28.6C with a mean of 28.4C. The mean cloacal temperature of the 31 snakes was 28.2C with a range from 26.5-30.8C. However when the snakes' cloacal temperatures were compared individually with water temperatures, only three snakes were within 0.2C of the water temperature, nine were warmer than the surface water (up to 2.4C).

FIG. 2. Thermal structure and bottom topography along a transect run perpendicular to the coast at Puerto Marquez, Mexico. The front or convergence is located between 7.2 and 8 km offshore. Pelamis were abundant along the edge of the front and farther offshore.

ISOCLINE DEPTH, M
BOTTOM DEPTH, M
20

40
60
80
100
120
200
400
600
800
15.5
15.0
15
151
15.0 15.0-15.0.
15.0
15.0°
14.5
14.5
14.5 14.5
14.5
14.5
14.2
14.3
130
3.2
14.1
1000
3.2
14.0
14.2
14.2
14.1
14.0
6.4
km from shore
14.0-14
8.8
page
849
6.4
8.8

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and 21 were cooler (up to 1.9C). On 18 July 1971, temperatures of 17 Pelamis in a slick in Bahía Manzanillo (Mexico) were measured with similar results: 10 snakes were 0.3-1.5C cooler than the sea surface, three were at the same temperature, and four were 0.1-1.6C warmer. This seems to be good evidence that significant amounts

of heat may be gained from solar radiation and that the snakes have a method of cooling, perhaps by diving. Several times snakes were collected in an area that had recently been cleared of snakes. This could be explained by the surfacing of snakes that had been diving at the time of the previous collection. A fisherman in Puerto Marquez (Guerrero), Mexico, who encountered sea snakes frequently, told us that the snakes were much more abundant during rains. This was true on two occasions when we had good catches on calm days during light showers. If the snakes dive only to cool themselves, there would presumably be no reason for them to do so when it was raining. Further work is obviously needed on the frequency and purpose of diving in Pelamis. Thermoregulation by diving is an attractive hypothesis since it serves to explain how a snake can successfully live in areas where environmental temperatures closely approach the upper lethal level.

Salinity tolerance

Most sea snakes are truly marine but there are at least three species living in freshwater or brackish water lakes, one in the Philippines and two in Rennell Island in the Solomon group (Loveridge 1946). Those species which normally live in seawater can live in freshwater. We have maintained a Laticauda semifasciata in freshwater for S months and seven Pelamis for 6 months, with no apparent ill effects. This does not mean that Pelamis is naturally found in brackish or freshwater areas. It is characteristic of areas where the salinity is close to that of normal seawater (about reported from estuaries of undetermined water and hypersaline coastal lagoons. No snakes were found in a freshwater lagoon (Laguna Coyuca) near Acapulco, even though they were abundant a few kilo meters offshore; at noon on 30 July and 1 August 1971, surface temperatures ranged from 31.5-33.0C. Although we did not coilect any snakes ourselves, fishermen at the town of Paredon (Chiapas) on Mar Muerto. a very large lagoon in the Isthmus of Tehuantepec (Mexico), reported that sea snakes were occasionally seen. The town is located at the outlet of the lagoon and

snakes could easily be washed in during storms. About 69 km up the lagoon a Punta Palmas (Oaxaca), where the wate was hypersaline (766 mM Cl, 48%), the fishermen reported that sea snakes were not present. The limits of tolerance of Pelamis and other sea snakes to hypersaline solutions have not been studied. The highest salinity recorded in our studies of natural populations was a value of 634 mM Cl (39.7%) at Salina Cruz (Oaxaca), Mexico Snakes were much more abundant at Acapulco where the concentration was lower (576-584 mM Cl, ~ 36%).

Concentration of snakes in slicks

About 8 weeks were spent in intensive study of populations of sea snakes in Mexico and Central America during July, August, and September 1970 and July and August 1971. Two patterns of distribution were commonly observed: The snakes appeared to be scattered on days when the water was rough and concentrated on calm days. In both cases the snakes were invariably seen lying motionless on the surface. On calm days large areas would lack snakes but persistent search would disclose numerous snakes in slicks into which they had ap parently drifted. It seems unlikely that the snakes actively seek out the slicks since the mechanism of slick formation makes it unnecessary for them to do so. The association with slicks is of great significance in under-
35%), although it has occasionally been standing the movements of these snakes since they seem to be passive and almost salinities (Shuntov 1966). During two trips planktonic in their response to water move- to Mexico we looked for Pelamis in fresh- ments.

Slick formation may be due to horizontal convergence of waterflow and winds (Ewing 1950). Internal waves were probably responsible for most of the slicks we saw. Slicks were visible as strips of smooth water from 0.5-5 m wide with variable amounts of terrestrial debris, foam, or both. Near Acapulco the slicks were not visible in the nearshore waters until the front or convergence was reached about 7.2-8 km offshore. This front is a point of marked transition from greenish, turbid, inshore water to transparent, blue, offshore water. On calm days slicks were commonly present

along the edge of the front and farther offshore; similar phenomena were observed farther to the south in Mexico and Costa Rica. At Acapulco Pelamis was not observed closer to the shore than the front. Since Pelamis seemed to be associated with the blue water on the seaward side of the front, a transect was taken on a line 1.6-8.8 km perpendicular to the headland at Puerto Marquez (near Acapulco) to determine the (Fig. 2). There was little difference in thermal structure and bottom topography of the front. Bathythermograph measure- either of these two parameters at the edge ments taken on either side of the front at Bahía Petacalco (Mexico) and Punta Salsipuedes (Costa Rica) showed a similar thermal structure of the blue and green water. Surface salinities were identical on either side of the front. In some cases the front was associated with a decrease in depth, but in other cases the bottom was relatively smooth.

At other localities (Golfo Dulce, Bahía Papagayo, and Bahía Culebra in Costa Rica; Bahía Banderas and Bahía Manzanillo in Mexico) either there was no green water or the front was very close to shore and Pelamis seemed to accompany the blue water even to within a hundred meters of shore in sheltered bays (Bahía Culebra and Bahía Manzanillo). The situation in Bahía Manzanillo is illustrated in Fig. 3. On three occasions a slick containing Pelamis was observed in the area shown. On 18 July 1971, 23 snakes were collected and released between 0900 and 1010 hours on a northward passage through this portion of the

BAHIA
SANTIAGO
PACIFIC OCEAN
BAHIA
MANZANILLO
MANZANILLO
LAGUN
CUYUTLAN

FIG. 3. A nearshore slick (solid circles and dotted line) containing 23 sea snakes near Manzanillo, Mexico. The depth is about 45 m and blue water touches the coast in this area. Sea snakes are sometimes washed ashore here.

slick. When the same path was retraced

between 1015 and 1045, only one snake was found. Thus the snakes caught originally had either dived or moved horizontally away from the slick. The close proximity of these snakes to the shore exposes them to the danger of being washed ashore. It is perhaps no coincidence that local residents report mass strandings of Pelamis on beaches all along this coast from time to time. Reputable observers described strandings along the Colima coast at Cuyutlán and Manzanillo and farther north in Jalisco at Bahía Tenacatita and Chamela. Strandings have been reported at various times of the year, including March and July, and seem in many cases to be associated with storms. Strandings apparently are a major source of mortality for Pelamis in certain areas.

The result of concentration of sea snakes by horizontally convergent water flows is shown in Fig. 4. On a calm day there may be hundreds or even thousands of snakes in a drift line or flotsam belt of this type. In a slick extending for about 3.2 km across the mouth of Golfo Dulce (Costa Rica) we

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FIG. 4. Horizontally convergent water flows have formed a slick containing floating debris and Pelamis. Small fish are seeking cover under the sea snakes and under vegetable refuse. This drift line or flot-
abundant food supply.
sam belt has many of the characteristics of a biological community and provides the sea snake with an

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captured 278 snakes in a few hours and there were many left. These lines of float-

ing debris are a sort of microhabitat since nutrient concentrations are believed to be ing vegetation (Forsbergh 1969). The cover high due to remineralization of decompos- provided by the debris also attracts a va- and Mitchell 1967, 1968). We believe this riety of fish and other marine life (Hunter stable and characteristic to be called a bio- logical community. The assemblage seems to be of great importance to the biology of Pelamis as it is a surface feeder on small assemblage of organisms to be sufficiently fishes (Klawe 1964). It catches fish, which are attracted to it as they are to a floating stick, by a rapid sideways strike.

of a concentrated line of Astrotia stokesii in the Strait of Malacca that was 3 m wide and 96 km long! Lowe estimated the num- bers of this snake in the millions and specu- lated that breeding or perhaps migration was in progress. It is probable that the process of concentration was by means of horizontally convergent water flows and that the snakes were in a slick since Lowe mentioned specifically that the sea surfact was unusually calm and oily in appearance and that there were masses of foam asso- ciated with the line of snakes.

In observations parallel with our own and published while this manuscript was in review, Kropach (1971) reported that Pelamis in the Gulf of Panama are com-

Pelamis is not unique among sea snakes monly found in slicks. Our findings regard in its drifting mode of life. An often quoted ing aggregation in slicks generally agree report by Lowe (1932) concerns a sighting with his.

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